

**Redescription of *Cambaroides japonicus* (De Haan, 1841)
(Crustacea: Decapoda: Cambaridae) with allocation of a type locality
and month of collection of types**

Tadashi Kawai and J. F. Fitzpatrick, Jr.*

(TK) Hokkaido Nuclear Energy Environmental Research Center, 261-1 Miyaoka, Kyowa,
Hokkaido 045-0123, Japan, e-mail: kawaita@fishexp.pref.hokkaido.jp;

(JFF) Museum of Natural History, Tulane University,
Belle Chasse, Louisiana 70037, U.S.A.

Abstract.—The Japanese crayfish, *Cambaroides japonicus* (De Haan), is re-described and illustrated, and details of its distribution and morphological variation are provided. Notable character differences between the populations of Honshu Island and Hokkaido Island indicate that gene flow between them is precluded. Analysis of geographical variation demonstrates that the undesignated type locality of the species is in central-western Aomori Prefecture, Honshu. The analysis of the gastrolith weights of the lectotype and possible topotypes indicates that the lectotype was collected in June.

The German medical doctor, Philip Franz von Siebold, was the first to introduce the natural history of Japan to European academics (Siebold 1897). He also taught European medicine to traditional Japanese practitioners, and on 23 February 1826, at Shimonoseki City, Yamaguchi Prefecture, received specimens of a crayfish used as a Japanese drug from his student, Kosai Yamaguchi (Siebold 1897). These were sent to the Netherlands and were described as *Cambaroides japonicus* by De Haan (1841). The brief description of the species included no locality or other collection data. Heretofore, taxonomic studies of *C. japonicus* have been limited to examining cyclic dimorphism (Kawai & Saito 1999), and the genus *Cambaroides* has yet to be the subject of modern morphological studies.

This paper provides a redescription of *C. japonicus*, allocates a type locality based on an analysis of geographic variation, and suggests a probable month of collection of

the types based on an analysis of monthly changes in gastrolith weight.

Abbreviations used in the text are: GVM, geographical variation in morphology; POCL, postorbital carapace length; RMNH, Nationaal Natuurhistorisch Museum, Leiden; and TCL, total carapace length.

Calculation of GVM: The geographical variation of each specimen was divided into three different levels (see Fig. 1), and the mean of the levels among specimens was calculated in each collection (Appendix I). The mean in each collection was classified into three degrees; 1.0–1.6, 1.7–2.3, 2.4–3.0.

Cambaroides japonicus (De Haan, 1841)

Fig. 2, Table 1

Diagnosis.—Body pigmented; eyes well developed, pigmented. Carapace subcylindrical, dorsal and lateral surfaces with large punctations, without tubercles; cervical spines absent. Rostrum acuminate, broadest at base; margins thickened, strongly convergent, lacking spines or tubercles; median carina present, often very weak;

* Deceased 11 July 2002.

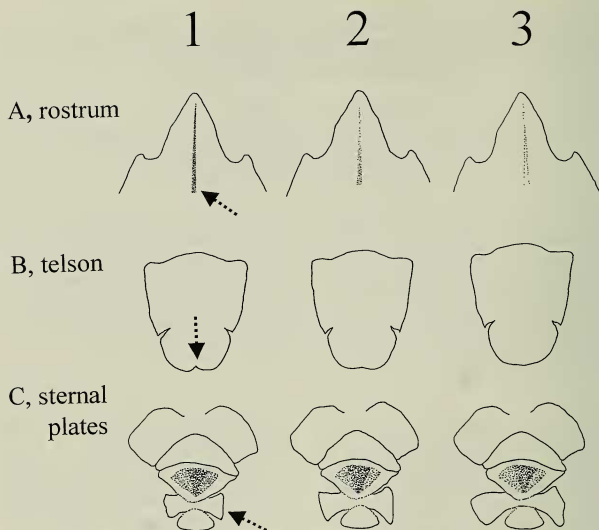


Fig. 1. Definition of morphological variations. A-1, median carina present on rostrum; A-2, carina intermediate between A-1 and A-3; A-3, carina almost absent. B-1, caudomedian excavation present on telson; B-2, excavation intermediate between B-1 and B-3; B-3, excavation absent; C-1, sternal plates closed; C-2, sternal plates intermediate between C-1 and C-3; C-3, sternal plates open.

acumen comprising 27.5–59.5% (\bar{X} = 47.8%, SD = 4.6, n = 200) of rostrum length, latter consisting 14.7–26.7% (\bar{X} = 17.3%, SD = 2.5, n = 200) of TCL. Areola 1.1–2.8 (\bar{X} = 1.9%, SD = 0.2, n = 200) times as long as broad, constituting 26.3–41.1% (\bar{X} = 29.5%, SD = 3.1, n = 200) of TCL and 30.9–46.9% (\bar{X} = 35.5%, SD = 3.3, n = 200) of POCL. Antennal scale 1.6–2.8 (\bar{X} = 2.2%, SD = 0.3, n = 100) times as long as broad, widest at midlength, lateral margin thickened, terminating in large, stout spine. Pleura of somites 2 and 3 with rounded to subtruncate ventral margins.

Palm of chela of cheliped with scattered

large punctations on dorsal, lateral, and ventral surfaces, without setae; palm inflated, width 1.2–1.6 (\bar{X} = 1.4%, SD = 0.1, n = 100) times length of mesial margin. Large punctations on dorsal, lateral and ventral surface of fixed finger and dactyl.

Hooks present on ischia of second and third pereopods in males, hooks simple and not reaching basioischial articulation. In situ gonopods (first pleopods) of adult male symmetrical, bases not contiguous. In mesial aspect (Fig. 2A), apex directed cephalodistally nearly 45° to axis of shaft, with strong endopodite and protopodite; apex (Fig. 2B) sclerotized, at least distally, ce-

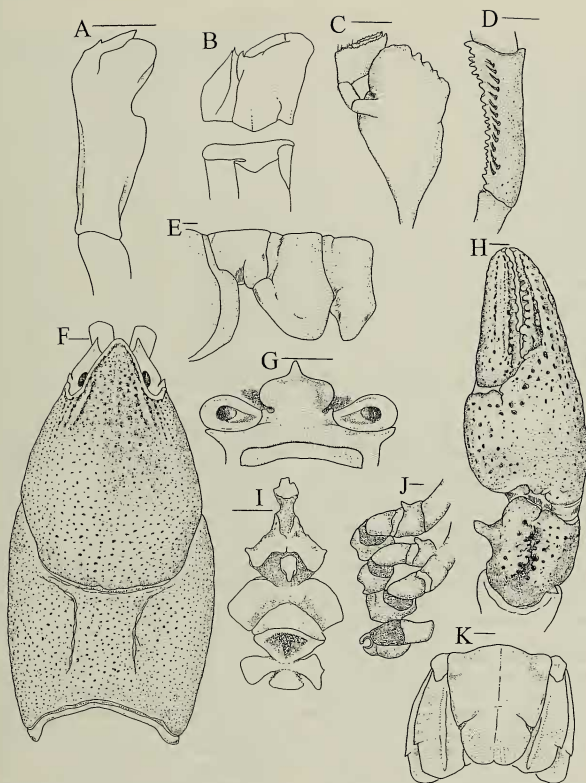


Fig. 2. *Cambaroides japonicus* (De Haan, 1841), all figures from lectotype (RMNH 5602, RMNH 5603), except B (redrawn from Hart 1953), I from paralectotype female (RMNH 2912), and J from paralectotype male #1: A, mesial view of first pleopod; B, mesial view of distal portion of first pleopod; C, lateral view of mandible; D, ventral view of ischium of third maxilliped; E, lateral view of first three abdominal segments; F, dorsal view of carapace; G, epistome; H, dorsal view of distal podomeres of right cheliped; I, annulus ventralis; J, proximal podomeres of pereopods; K, dorsal view of telson and uropods. Line = 2 mm.

Table 1.—Measurements of type series of *Cambaroides japonicus*.

	Lectotype	Paralectotype male #1	Paralectotype male #2	Paralectotype female
Carapace				
Total length	31.6	22.1	21.7	30.4
Postorbital length	25.4	18.6	17.6	25.1
Width	16.4	11.1	11.7	15.1
Height	11.1	8.7	9.4	11.1
Areola				
Length	9.8	7.3	7.0	9.4
Width	4.9	3.7	2.6	4.2
Rostrum				
Length	6.6	4.7	4.3	7.1
Width	7.3	4.9	4.5	7.3
Chela				
Length of mesial margin of palm	10.9	6.9	5.6	8.9
Width of palm	11.4	7.6	7.3	8.9
Length of lateral margin	24.5	16.4	15.8	20.4
Length of dactyl	14.2	8.3	8.0	10.8
Abdomen width	14.7	10.6	10.2	17.3

phalolaterally swollen into straight, subacute, stout, cephalodistally directed mesial process, cephalic process, and central projection with blade-like caudal process; 3 subequal spines near mid-width of apex, length about one-tenth of width of apex. Proximal part of gonopod subcylindrical in cross section, becoming subtriangular distally. Sperm groove along caudomesial face of gonopod shallow, open between mesial process and central projection, ending in relatively blunt tip. Adult male gonopod with "juvenile suture".

Annulus ventralis (Fig. 2I) immovable, symmetrical, rounded in outline, about 1.2 times as long as wide. Preannular plate transversely subdivided into 2 subtriangular plates, cephalic margin of anterior part broadly attached to preceding sternite, middle section of posterior part with shallow depression as fossa without sinus. Postannular sclerite subcircular, about 1.7 times as broad as long, and 0.5 times as wide as annular plate.

Measurements of type specimens provided in Table 1.

Description of lectotype.—Cephalotho-

rax (Fig. 2F) subcylindrical, slightly compressed laterally; dorsoventrally depressed (greatest width of thoracic section 1.5 times depth); POCL 80.4% of TCL. Areola 2.0 times longer than wide, dense punctate, length 31.0% of TCL (38.6% of POCL). Rostrum acuminate, tip barely reaching distal margin of antennal scale and midlength of ultimate podomere of antennal peduncle; acumen comprising 48.4% of rostrum length, latter consisting 20.9% of TCL; floor (dorsal surface) of rostrum dense punctate; median carina nearly absent.

Postorbital ridges poorly defined. Suborbital angle obtuse, without tubercle or spine. Antennal scale with strong distolateral spine, tip reaching tip of rostrum and midlength of ultimate podomere of antennal peduncle.

Greatest width of abdomen 89.6% greatest width of carapace. Proximal podomere of uropod lacking spine or tubercle on lateral lobe, mesial lobe broadly rounded; mesial ramus of uropoda with caudolateral spine, and submedian dorsal ridge terminating in small caudomedian spine, tip of which not reaching caudal margin; lateral

ramus with stout caudolateral spine; lateral ramus divided into cephalic and caudal sections, separated by transverse flexure bearing spines. Telson divided into cephalic and caudal sections, each caudolateral corner with pair of stout, fixed spines. Caudal margin of telson with deep median excavation.

Epistome (Fig. 2G) with subovate cephalic lobe bearing prominent cephalomedian projection, margins of lobe markedly elevated; fovea of epistome scarcely visible; central portion of epistome with pair of transverse grooves, and deep transverse grooves along cephalic margin of weakly arched zygoma. Third maxilliped (Fig. 2D) with mesial margin bearing 21 denticles; mesial half of ischium with row of clusters of long, stiff setae. Incisor ridge of right margin (Fig. 2C) with 5 corneous denticles.

Palm of right chela (Fig. 2H) subovate in cross section, moderately depressed dorsoventrally. Total chela length 77.5% of TCL. Palm 2.1 times as long as wide, length of mesial margin 44.5% of total chela length; dorsal surface with deep, widely scattered punctations, which become scarce laterally and caudolaterally; ventral surface less punctate. Dorsal surface of both fingers with poorly defined, longitudinal submedian ridge, and rows of deep punctations; tip of fingers corneous, subacute. Opposable surface of fixed finger with row of 9 tubercles, third from base largest. Opposable surface of dactyl with row of 5 tubercles; length of dactyl 1.3 times length of mesial margin of palm. Carpus (Fig. 2H) longer than broad, dorsal surface with prominent longitudinal furrow, lateral and mesial surface with large, crowded punctations; mesial surface with large, blunt subdistal spine, lateral surface with proximal spine; ventral surface with oblique furrow, short longitudinal furrow, and deep punctations. Merus with row of prominent tubercles on ventromesial margin, punctuate dorsally and ventrally.

Gonopods as described in "Diagnosis". In addition, tips of gonopods extending be-

yond cephalic margin of coxae of fourth pereopods.

Description of paralectotype male#1.—Differing from lectotype as follows: greatest width of thoracic section 1.3 times depth. POCL 84.2% of TCL. Areola length 33.0% of TCL (39.2% of POCL). Acumen comprising 46.1% of rostrum length, latter consisting 21.3% of TCL. Greatest width of abdomen 95.5% greatest width of carapace. Total chela length 74.2% of TCL; palm of right chela 2.2 times as long as wide; length of mesial margin 42.1% of total chela length. Dactyl length 1.2 times length of mesial margin of palm; opposable surface of fixed finger with 10 tubercles; opposable surface of dactyl with 6 tubercles.

Description of paralectotype—female.—Differing from lectotype, except in secondary sexual characteristics, as follows: greatest width of thoracic section 1.4 times depth. POCL 82.6% of TCL. Areola 2.2 times as long as broad. Areola length 30.9% of TCL (37.5% of POCL). Acumen comprising 50.0% of rostrum length, latter consisting 23.4% of TCL. Opposable surface of fixed finger with 6 tubercles, proximal largest; opposable surface of dactyl with 6 tubercles, length of finger 1.2 times length of mesial margin of palm.

Disposition of types.—All dry and lacking most appendages. Lectotype: 1 male, RMNH 5602, RMNH 5603. Paralectotypes: 2 males and 1 female, RMNH 2912. The lectotype has the mark "♀" written on the areola, but is a male. A milky-white gastrolith is included with the lectotype. Its dry weight (dried at 80°, 48 hr) is 0.0305 g, and its shape is semi-globular, with the greatest diameter 4.5 mm, the least diameter 4.2 mm, and the greatest height 1.8 mm.

Type locality.—No type locality for *C. japonicus* has ever been designated. In order to establish a type locality, we examined geographic variation in morphology (GVM) to identify any unique characters that might be displayed by the type specimens. Earlier, Fitzpatrick (1995) detected possible geographically defined races based

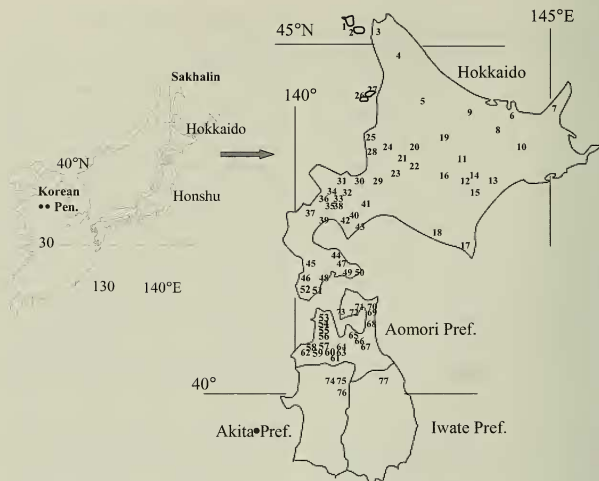


Fig. 3. Known geographical range of *Cambaroides japonicus* (De Haan, 1841). Numbers correspond to sampling sites listed in Appendix I.

on a distinct rostral carina and pleural margin shape of the abdominal segment. Samples, however, were too small and too widely scattered for definite conclusions. In our larger series from far more localities, we examined the presence or absence of a median carina on the rostrum, median excavation in the caudal margin of the telson, and open or closed sternal plates. The GVM was classified into three levels (Fig. 1), and mean GVM in each collection was summarized according to three categories by previously mentioned calculation (Fig. 4). Three GVM characters were found to be common in all the type series specimens, and similar to characters found only in specimens from central-western Aomori Prefecture, Honshu (Figs. 1–4, Appendix I, 55–62). This strongly suggests that the type

specimens were collected in that area. The central western Aomori Prefecture was designated as a probable locality of the type series. Kurimi (1811) and Ohtsuki (1817), in a paper published at the time Siebold received specimens of *C. japonicus*, remarked that the species commonly inhabited central-western Aomori Prefecture. This lends support to our assumption about the type locality.

Date of type collection.—Monthly samplings of *C. japonicus* were made from April to November 1989 in Iwaki City (Fig. 3, Appendix I, 59), in the central-western part of Aomori. For each sampling, gastroliths were removed from the stomachs of 30 individuals, ranging in size from 17.7 mm to 25.4 mm POCL, which corresponds to size range of the types. The result indi-

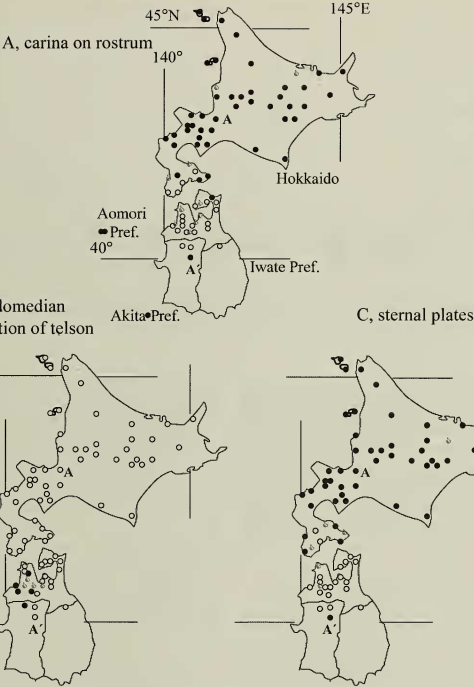


Fig. 4. Geographical variation of (A) carina on rostrum, (B) caudomedian excavation of telson, and (C) sternal plates. Solid circle, 1.0–1.6 level of mean GVM in collection; semi-open circle, 1.7–2.3; open circle, 2.4–3.0. A, Sapporo City; A', Kazuno City.

cates that the dry weight (dried at 80°, 48 hr) of the gastrolith from lectotype (0.0305 g) is similar to that of the June sample (Fig. 5). Thus, it is believed the type series was likely collected in June.

Range and specimens examined.—We examined a total of 405 specimens from Hokkaido Islands and four of its larger

nearby islands (Rebun, Rishiri, Teuri, and Yagishiri), as well as the northern part of Honshu Island (major parts of Aomori Prefecture, and northern part of Akita and Iwate Prefecture). Information on sampling sites is provided in Fig. 3 and Appendix I.

As far as known, *C. japonicus* is endemic to the entire Japanese Archipelago. How-

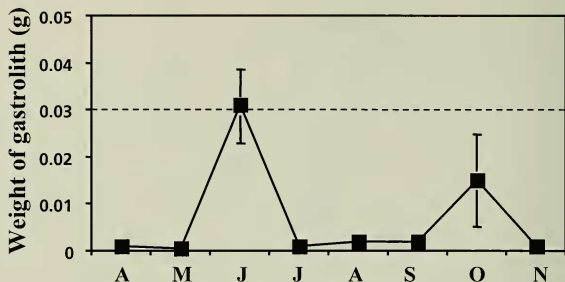


Fig. 5. Monthly change of dry gastrolith weight in *Cambaroides japonicus* (De Haan, 1841) from Iwaki City, Aomori Prefecture (see Fig. 3, 59). Vertical bar indicates SD. Dotted horizontal line shows the dry gastrolith weight of the lectotype (0.0305 g).

ever, Okada (1933:155–156) mentioned that “Mr. T. Urita, a director of the Girl’s High School at Maoka in south part of Sakhalin, U.S.S.R., informed me that *C. japonicus* seems not to occur in the stream and rivers, and that if it is found in anywhere in Sakhalin, it is very rare; however, I examined Outomari of Sakhalin specimens in the collection of Professor Iijima of Tokyo Imperial University, these are preserved in the Zoological Institute, Faculty of Sciences, Tokyo Imperial University”. And Urita (1942:39) said “I consequently spent considerable time and labour in search of this species, especially in Outomari and its neighbourhood, but unfortunately, without success; presumably, this species does not exist here in south Sakhalin, not, at any rate, at present”. On 11 November 2001, all specimens in the Tokyo Imperial University were transferred to the University Museum, the University of Tokyo, but no specimen from the Sakhalin could be found there.

Size.—The largest lake specimen is a male from Lake Akan, Hokkaido, measuring 39.2 mm POCL; the largest brook specimen is a male from Hamamasu with a

POCL of 34.3 mm. The smallest ovigerous female is 17.6 mm POCL.

Variation.—Most variations were noted in the number and comparative sizes of tubercular ornamentation, particularly on the cheliped. The caudolateral corner of the cephalic section of the telson bears one to three fixed spines. The lateral margin of the telson of most specimens gently tapers to a rounded caudal margin, but in some the lateral margins are subparallel and the caudal margin is flat. Some specimens have bosses between the sternal plates (Fig. 2I), but in most specimens these bosses are nearly absent.

Color.—Dorsal and lateral surfaces of cephalothorax, abdomen, chelae, and tail fan dark brown to chocolate, ventral surface light brown. Ventral surface of chela dark orange. Tips of pereopods dark orange. Caudal process and three spines of distal adult male gonopods amber. Background colors translucent to light brown in freshly molted individuals. The whitish-blue colorations or “blue color phase” (Fitzpatrick 1987) on the dorsal and lateral surfaces of thoracic carapace, abdomen, chelae, and tail fan, was found in specimens from Abashiri,

Obihiro, Iwamisawa, and Hamamasu, Hokkaido Prefecture, and in Shichinohe, Aomori Prefecture (see Appendix I).

Crayfish associates and conservation status.—During the past decade, local extinctions of *C. japonicus* have been reported from throughout its range. In eastern Hokkaido its numbers have been declining rapidly, while population numbers of the introduced crayfish, *Pacifastacus leniusculus* (Dana, 1852) in the same area have been increasing (Kawai et al. 2002). Also, Kawai et al. (2002) demonstrated that following the introduction of *P. leniusculus* into Lake Kussharo and Lake Shikaribetsu, *C. japonicus* disappeared. *Pacifastacus leniusculus* is known to be a vector of crayfish plague fungus, *Aphanomyces astaci* (Schikora), to which it is resistant, but to which *C. japonicus* is highly susceptible (Unestam 1969). It is possible that *Aphanomyces* may be a factor affecting displacement of *C. japonicus* at some localities, but there is as yet no investigation of infection to the natural populations in Hokkaido. The mechanisms underlying the negative impacts of *P. leniusculus* on *C. japonicus* required further investigation.

Cambaroides japonicus was designated an endangered species by the Japanese Fisheries Agency in 1995 and by the Japanese Environmental Agency in 2000.

Ecological notes.—*Cambaroides japonicus* appears to be restricted to lentic habitats, either lakes or small brooks in which current velocity is less than 10.0 cm/sec. In brooks, the species is found beneath boulders, or burrows in the banks. It appears to be a secondary burrower, and retreats underground to remain below the frost line in winter. Females enter burrows prior to ovulation, and remain in them to lay eggs. Most burrows are Y- or T-shaped, with two openings slightly above or below the water surface.

Reproduction.—Mating in *C. japonicus* is unique (Kawai & Saito 2001). The male moves beneath the female to deposit its spermatophore, and does not grasp the fe-

male with its chelae. In Hokkaido, mating pairs were encountered only in September and October, and ovigerous females during the subsequent May. Spermatozoa obviously are stored in the annulus ventralis for a six-month period during winter. Number of ova ranges from 50 to 100, and egg diameter is 2.3–2.7 mm.

Name in Japanese.—In Japan, it is usual for organisms to have one or more local names. To prevent possible ambiguity in this pragmatic system, and make it easier to incorporate taxonomic and distributional information, the common, Japanese name Zarigani, is proposed. This name, which refers to an animal that moves backward (Ohtsuki 1817), is also mentioned in older papers (e.g., Kurimi 1811). The names “Sarugani” which is the local name in Aomori Prefecture, and “Sarukani,” the local name in Akita Prefecture, means “the backward creeping crab.” Two local names are on the label attached to the specimens of *C. japonicus* at Saito Ho-Onkai Museum, Sendai, Japan (Nos. 1039, 1369). Also, the Ainu people, former occupants of Hokkaido and northern Honshu, know *C. japonicus* as “Tekinpekorupe,” alluding to an armed knight (Ohtsuki 1817).

Discussion

Cambaroides japonicus occurs in northern parts of Honshu and Hokkaido Islands (Fig. 3). It is likely that populations of the species inhabiting certain areas of Honshu were introduced from Hokkaido, but differences in the GVM (Fig. 4, Appendix I) indicate that the majority of populations on Honshu are native. An exception is seen in the GVM of specimens from Kazuno City (A'), Akita Prefecture, Honshu, which agrees with that of Sapporo City (A), Hokkaido. In 1943, a locality report in a small stream in Kazuno City originated from introduction of a population in Sapporo City (Mr. T. Komoriya, Japanese regional report 1978).

The distribution of Asian branchiobdel-

lidans, which are symbionts on crayfish, including *C. japonicus*, may shed some additional light on this issue, since there is a high degree of endemism in the various species. *Cirrodriulus aomorensis* and *C. tsugarensis* occur in Honshu (Gelder & Ohtaka 2000), while *C. inukaii* and *C. uchidai*, and others occur only in Hokkaido (Yamaguchi 1934). There is no overlap in the natural distributions of these two species. However, *C. inukaii* and *C. uchidai* have both been found in Kazuno City, Akita Prefecture, northern Honshu, an occurrence that might be explained by an introduction of *C. japonicus* from Hokkaido (Gelder & Ohtaka 2000).

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Appendix 1.—Sampling data and geographic variation of morphology in *Cambaroides japonicus*.

Sampling site (No. ref. to Fig. 3)		Date	Specimens	POCL ± SD	Rostrum	Telson	Sternal plates
1	Rebun	04 Sep 1968	♂3 ♀2	21.3 ± 2.9	1.0 ± 0.0	3.0 ± 0.0	1.0 ± 0.0
2	Rishiri	17 Nov 1992	♂1 ♀1	22.3 ± 4.8	1.5 ± 0.7	3.0 ± 0.0	1.0 ± 0.0
3	Wakkanai	11 Aug 1998	♂4 ♀1	22.2 ± 2.8	1.2 ± 0.4	2.8 ± 0.4	1.0 ± 0.0
4	Nakagawa	16 Aug 1990	♂1 ♀0	20.2 ± 0.0	1.0 ± 0.0	3.0 ± 0.0	—
5	Shibetsu	01 Sep 1957	♂1 ♀1	16.1 ± 2.0	1.0 ± 0.0	3.0 ± 0.0	1.0 ± 0.0
6	Abashiri	04 July 1982	♂0 ♀2	22.3 ± 2.3	1.0 ± 0.0	2.5 ± 0.7	1.0 ± 0.0
7	Utoro	18 Aug 1999	♂3 ♀1	19.2 ± 1.5	1.3 ± 0.5	2.5 ± 1.0	2.0 ± 0.0
8	Tsubetsu	25 Apr 1987	♂2 ♀0	23.1 ± 6.2	1.0 ± 0.0	3.0 ± 0.0	2.0 ± 0.0
9	Maruseppu	10 Aug 1998	♂2 ♀1	21.0 ± 4.1	1.7 ± 0.6	3.0 ± 0.0	1.0 ± 0.0
10	Akan	04 Aug 1933	♂1 ♀2	26.8 ± 10.8	1.0 ± 0.0	3.0 ± 0.0	1.0 ± 0.0
11	Shikaoi	14 May 1987	♂6 ♀1	26.9 ± 8.4	1.0 ± 0.0	3.0 ± 0.0	1.0 ± 0.0
12	Memuro	04 Aug 1986	♂0 ♀1	24.5 ± 0.0	1.0 ± 0.0	3.0 ± 0.0	1.0 ± 0.0
13	Ikeda	25 Sep 2000	♂0 ♀1	13.2 ± 0.0	1.0 ± 0.0	3.0 ± 0.0	1.0 ± 0.0
14	Otofuke	25 Sep 2000	♂1 ♀0	1.97 ± 0.0	1.0 ± 0.0	3.0 ± 0.0	—
15	Obihiro	08 May 1986	♂1 ♀0	19.2 ± 0.0	1.0 ± 0.0	3.0 ± 0.0	—
16	Shintoku	09 Aug 1998	♂0 ♀1	15.4 ± 0.0	1.0 ± 0.0	3.0 ± 0.0	1.0 ± 0.0
17	Erimo	19 Sep 2000	♂2 ♀1	18.8 ± 0.5	1.0 ± 0.0	3.0 ± 0.0	1.0 ± 0.0
18	Monbetsu	20 July 1990	♂4 ♀0	18.5 ± 2.3	1.0 ± 0.0	2.5 ± 0.6	—
19	Kamikawa	20 Sep 2000	♂1 ♀1	21.4 ± 4.9	1.0 ± 0.0	3.0 ± 0.0	1.0 ± 0.0
20	Biei	07 Aug 1998	♂1 ♀1	25.3 ± 3.3	1.0 ± 0.0	3.0 ± 0.0	1.0 ± 0.0
21	Akabira	08 Aug 1999	♂1 ♀0	19.6 ± 0.0	1.0 ± 0.0	3.0 ± 0.0	—
22	Furano	08 Aug 1999	♂2 ♀2	18.5 ± 3.0	1.0 ± 0.0	3.0 ± 0.0	1.0 ± 0.0
23	Iwamisawa	27 May 1959	♂2 ♀3	18.7 ± 1.0	1.0 ± 0.0	2.8 ± 0.5	1.0 ± 0.0
24	Takikawa	11 Aug 1992	♂1 ♀1	20.2 ± 2.1	1.0 ± 0.0	2.5 ± 0.9	1.0 ± 0.0
25	Ofuyu	23 Aug 1992	♂0 ♀1	20.0 ± 0.0	2.0 ± 0.0	3.0 ± 0.0	1.0 ± 0.0
26	Teuri	29 July 2002	♂5 ♀5	21.6 ± 2.0	1.2 ± 0.4	3.0 ± 0.0	1.2 ± 0.5
27	Yagishiri	29 July 2002	♂5 ♀5	20.4 ± 1.6	1.5 ± 0.5	3.0 ± 0.0	1.0 ± 0.0
28	Hamamasu	17 June 2000	♂5 ♀3	20.7 ± 3.0	1.0 ± 0.0	3.0 ± 0.0	1.0 ± 0.0
29	Sapporo	03 Nov 1990	♂4 ♀5	23.5 ± 2.6	1.3 ± 0.4	3.0 ± 0.0	1.2 ± 0.5
30	Otaru	03 June 1999	♂5 ♀6	20.9 ± 2.7	1.0 ± 0.0	3.0 ± 0.0	1.1 ± 0.4
31	Yoichi	28 Aug 2001	♂5 ♀5	18.8 ± 1.3	1.0 ± 0.0	3.0 ± 0.0	1.0 ± 0.0
32	Kucchan	07 Oct 2000	♂5 ♀5	21.3 ± 2.8	1.0 ± 0.0	3.0 ± 0.0	1.0 ± 0.0
33	Niseko	08 Oct 2000	♂5 ♀5	21.6 ± 2.7	1.1 ± 0.4	3.0 ± 0.0	1.0 ± 0.0
34	Kyowa	10 Oct 1998	♂4 ♀6	21.8 ± 2.7	1.1 ± 0.4	3.0 ± 0.0	1.3 ± 0.5
35	Rankoshi	21 July 2001	♂5 ♀5	19.0 ± 2.7	1.6 ± 0.5	3.0 ± 0.0	1.0 ± 0.0
36	Iwanai	01 July 2001	♂6 ♀4	19.2 ± 1.8	1.0 ± 0.0	3.0 ± 0.0	1.0 ± 0.0
37	Suttsu	13 Sep 2001	♂5 ♀5	20.5 ± 4.2	1.0 ± 0.0	3.0 ± 0.0	1.0 ± 0.0
38	Kyogoku	28 Sep 2001	♂4 ♀6	22.3 ± 1.9	1.4 ± 0.5	3.0 ± 0.0	1.0 ± 0.0
39	Oshamanbe	19 Sep 2001	♂3 ♀5	19.7 ± 2.2	1.4 ± 0.5	3.0 ± 0.0	1.2 ± 0.4
40	Chitose	02 Aug 1999	♂2 ♀5	21.0 ± 2.5	1.5 ± 0.5	3.0 ± 0.0	1.0 ± 0.0
41	Eniwa	04 Nov 2001	♂2 ♀2	20.3 ± 2.5	1.0 ± 0.0	3.0 ± 0.0	1.0 ± 0.0
42	Soubetsu	02 Aug 1998	♂1 ♀0	20.7 ± 0.0	1.0 ± 0.0	3.0 ± 0.0	1.0 ± 0.0
43	Shiraoi	12 Aug 1990	♂0 ♀3	18.8 ± 1.7	1.0 ± 0.0	3.0 ± 0.0	1.0 ± 0.0
44	Sahara	01 Aug 1998	♂2 ♀1	21.5 ± 2.0	2.3 ± 0.6	3.0 ± 0.0	2.0 ± 0.0
45	Assabu	23 June 1997	♂4 ♀3	20.3 ± 2.5	1.4 ± 0.5	3.0 ± 0.0	2.7 ± 0.6
46	Kaminokuni	22 June 1997	♂1 ♀1	22.4 ± 1.5	2.0 ± 0.0	3.0 ± 0.0	1.0 ± 0.0
47	Shikabe	23 Aug 1998	♂1 ♀4	22.2 ± 2.1	2.6 ± 0.5	2.4 ± 0.5	1.5 ± 0.6
48	Kikonai	22 June 1997	♂2 ♀7	20.4 ± 1.7	2.7 ± 0.5	3.0 ± 0.0	2.6 ± 0.6
49	Toi	20 Aug 1992	♂2 ♀7	19.9 ± 1.0	1.0 ± 0.0	3.0 ± 0.0	1.4 ± 0.5
50	Todohokke	23 June 1997	♂5 ♀7	20.7 ± 2.5	1.1 ± 0.3	3.0 ± 0.0	2.1 ± 0.4
51	Fukushima	22 June 1997	♂3 ♀7	21.7 ± 2.1	2.4 ± 0.8	3.0 ± 0.0	2.1 ± 0.4
52	Matsumae	22 June 1997	♂7 ♀5	23.4 ± 3.2	2.6 ± 0.8	2.6 ± 0.6	1.6 ± 0.5
53	Imabetsu	05 Aug 1998	♂1 ♀4	22.0 ± 1.4	2.2 ± 0.8	2.8 ± 0.4	2.0 ± 0.0
54	Shiura	30 Aug 1997	♂2 ♀0	20.9 ± 2.3	2.0 ± 1.4	3.0 ± 0.0	—

Appendix I.—Continued.

	Sampling site (No. ref. to Fig. 3)	Date	Specimens	POCL \pm SD	Rostrum	Telson	Sternal plates
55	Nakasato	21 Nov 1999	♂1 ♀1	22.5 \pm 2.5	2.5 \pm 0.7	1.5 \pm 0.7	3.0 \pm 0.0
56	Kanagi	07 Oct 2000	♂0 ♀2	20.3 \pm 0.4	3.0 \pm 0.0	2.0 \pm 1.4	2.5 \pm 0.7
57	Goshogawara	19 Sep 1998	♂7 ♀4	19.2 \pm 2.4	2.3 \pm 0.5	2.0 \pm 0.9	2.5 \pm 0.6
58	Kizukuri	22 Aug 1999	♂8 ♀2	23.7 \pm 2.2	2.7 \pm 0.5	2.7 \pm 0.7	2.0 \pm 0.0
59	Iwaki	26 July 1998	♂6 ♀0	21.3 \pm 2.6	2.7 \pm 0.6	1.5 \pm 0.8	—
60	Hirosaki	30 Sep 1997	♂2 ♀2	19.8 \pm 2.2	3.0 \pm 0.0	2.0 \pm 1.0	3.0 \pm 0.0
61	Ikarigaseki	04 Oct 1931	♂2 ♀5	17.6 \pm 2.2	2.7 \pm 2.2	2.6 \pm 0.5	3.0 \pm 0.0
62	Ajigasawa	12 Aug 1998	♂2 ♀2	20.1 \pm 2.3	2.8 \pm 0.5	1.5 \pm 1.0	3.0 \pm 0.0
63	Namioka	22 June 2000	♂4 ♀1	21.3 \pm 1.9	2.8 \pm 0.4	2.2 \pm 0.8	3.0 \pm 0.0
64	Aomori	03 May 1998	♂7 ♀3	20.7 \pm 3.4	1.9 \pm 0.6	2.8 \pm 0.4	2.7 \pm 0.6
65	Hiranai	10 Oct 2000	♂2 ♀3	19.4 \pm 2.1	2.4 \pm 0.5	3.0 \pm 0.0	3.0 \pm 0.0
66	Tenmabayashi	14 July 1994	♂0 ♀2	18.6 \pm 1.7	3.0 \pm 0.0	3.0 \pm 0.0	3.0 \pm 0.0
67	Shichinohe	22 June 1999	♂2 ♀1	15.2 \pm 1.6	2.7 \pm 0.6	3.0 \pm 0.0	3.0 \pm 0.0
68	Yokohama	23 May 1999	♂1 ♀0	19.4 \pm 0.0	3.0 \pm 0.0	3.0 \pm 0.0	—
69	Higashidouri	27 Aug 1999	♂2 ♀2	19.0 \pm 1.4	2.5 \pm 0.6	3.0 \pm 0.0	3.0 \pm 0.0
70	Mutsu	27 Aug 1999	♂1 ♀1	23.0 \pm 0.7	2.5 \pm 0.7	3.0 \pm 0.0	3.0 \pm 0.0
71	Ouhata	22 June 1999	♂1 ♀5	18.3 \pm 0.8	1.2 \pm 0.4	3.0 \pm 0.0	2.6 \pm 0.5
72	Kawauchi	05 June 1998	♂0 ♀2	21.4 \pm 1.7	2.0 \pm 1.4	3.0 \pm 0.0	2.5 \pm 0.7
73	Wakinosawa	17 May 1998	♂3 ♀0	18.3 \pm 0.9	3.0 \pm 0.0	3.0 \pm 0.0	—
74	Tashiro	21 June 1991	♂0 ♀2	7.5 \pm 0.3	3.0 \pm 0.0	1.5 \pm 0.0	3.0 \pm 0.0
75	Ohdate	24 Aug 2002	♂3 ♀7	21.9 \pm 3.9	3.0 \pm 0.0	3.0 \pm 0.0	3.0 \pm 0.0
76	Kazuno	23 June 1990	♂7 ♀2	18.9 \pm 1.1	1.3 \pm 0.5	3.0 \pm 0.0	1.0 \pm 0.0
77	Ninohe	22 June 1999	♂1 ♀2	18.3 \pm 1.2	2.7 \pm 0.6	2.7 \pm 0.6	3.0 \pm 0.0

—: not measured.